AN ANALYSIS OF MOTOR FUNCTION AND CONTROL IN THE HUMAN NERVOUS SYSTEM

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THESIS

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AND CONTROL
IN THE HUMAN NERVOUS SYSTEM

by

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by

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ABSTRACT

A theory is presented on voluntary learned and unlearned motor movement. The basic elements on motor control are presented, analyzed, and discussed. These include fundamental reflexes, gamma-muscle spindle servo mechanism, reticular system, cerebellum, and higher brain centers. The interrelations between the above elements and systems are examined in detail as a basis of the theory presented. The theory follows the transition from unlearned to learned movement and demonstrates how detailed control may be modified by the cerebellum and associated areas.

TABLE OF CONTENTS

LIST OF FIGURES

I. INTRODUCTION

A. BIOENGINEERING

The field of bioengineering is a relatively new field and as such it is not inappropriate to devote a separate introduction to it in addition to the thesis itself.

The human being is one of the most complex systems ever created and interest in man has generated a variety of disciplines which can be divided into two groups. First, professions that can trace their origins to the study of human beings, such as; medical practitioners, psychiatrists, psychologists, and physiologists. The second group consists of other fields that have seized the opportunity to apply their particular skills to the study of living systems. Professions in this group generally retain the name of the parent field, but prefixed with the word bio; such as, biochemists and biophysicists.

The field of bioengineering is one of the newest members of the family, the reason being historical. The engineering disciplines were primarily concerned with deterministic systems which could be exposed or analyzed with existing instruments and mathematics. With the advent of more sophisticated technology and a desire to explore more challenging areas it became obvious the most lucrative targets were living systems; in particular, the human being. Thus, bioengineering can be defined as

the application of sound engineering principles to the study of living systems; in particular, improving the interface of man to his environment.

B. MOTOR CONTROL

Models of physical systems are more or less precise descriptions; for example, a mathematical description of the dynamics of the planetary system. The most serious shortcoming in constructing models is insufficient understanding of underlying processes or signal flows. The motor system in addition to other portions of the nervous system is an immense conglomerate of interconnected neurons, a considerable portion of which is well understood and documented (Fig. 3). The difficulty arises in that there are significant gaps, particularly in correllating function to anatomy.

The overall objective of this thesis is to provide sufficient background material on motor movement to present a theory of voluntary movement. The difficulty and frustration of presenting a theory or postulates on a system as complicated as the human nervous system is that regardless of how well it may explain the majority of observations there is always the exception. This should not be viewed as a hindrance for it is the exceptions that test and modify theories. Another difficulty arises in the connotation of words themselves and care was taken throughout in an attempt to minimize misinterpretation.

II. MOTOR MOVEMENT

For purposes of this paper movement is any change between static states. The body can assume static states, but it must be remembered the nervous system is dynamic; i. e., neuronal activity is continually occurring even though there appears to be a lack of movement. Posture is the spatial orientation of the body with respect to itself; i. e., a person with arms and legs extended can maintain that particular posture regardless whether standing or lying down. A changing posture will be referred to as postural movement. Equilibrium is the relationship of the whole body to the external environment; thus a change in equilibrium implies translational or rotational movement. Balance is a specific form of equilibrium as it is present only in a gravitational field and involves rotation with respect to the gravitational vector.

Based on the definitions chosen and an extensive search of existing literature the following assumptions are proposed as an initial foundation. Everyday movement can be segregated into a voluntary and reflexive component. Voluntary movements may utilize, modify or inhibit reflexes, are purposeful, require the services of the cerebral cortex, and can be learned. Reflexes develop with growth of the nervous system, are integrated at various levels, are not purposeful, may or may not utilize the cerebral cortex, and are not learned. Reflexes of posture or equilibrium cannot occur independently and must be coordinated.

III. ELEMENTS OF MOTOR CONTROL SYSTEMS

A. NEURONS

The nervous system is composed of special types of cells called neurons. These cells contain a nucleus but unlike other cells they have dendrites and an axon which may also give off collaterals. These cells have the property of propogating a changing membrane potential (action potential or impulse) down the length of the axon. This impulse is all or nothing - meaning once generated it will be propogated without attenuation (energy being provided locally). When the impulse reaches the presynaptic terminals (end of an axon or collateral) a chemical substance is released. The release point is called a synapse and is the junction between presynaptic terminals and either dendrites or the soma (cell body proper which includes the nucleus). The chemical released is either excitatory or inhibitory dependent on whether its influence is to lower the postsynaptic membrane potential (excitatory) or to increase it (inhibitory). If the resting membrane potential in the soma is decreased to a threshold level an action potential will be generated. The threshold level can be achieved by temporal or spatial summation since one incoming impulse is normally not sufficient.

The overall nervous system is a highly organized complex of three types of neurons; affectors, effectors, and interneurons. All information

transmitted or processed in the nervous system is by the impulse activity of these neurons. The affectors instead of having dendrites have transducers that translate sensory information into impulses. Effectors serve the opposite function of causing some action, and interneurons are self explanatory.

B. MOTONEURONS

Alpha and gamma motoneurons (effectors) innervate muscle fiber and release a chemical transmitter which causes contraction of the muscle fiber. The alpha type of motoneuron is associated with skeletal muscle; whereas, the gamma type innervates a special servo system called the muscle spindle.

C. SENSORY INPUT

The nervous system in performing its motor function requires sensory input (affectors) to be appraised of current posture and equilibrium.

Proprioceptors are concerned with skeletal and muscular states. The primary and secondary afferents of the muscle spindle provide information on the length and rate of contraction. Tendon organs provide information on muscular tension. Joint receptors provide information on skeletal configuration.

Exteroceptors provide information regarding the surface of the body, and for the purpose of motor function pressure and touch are the most significant.

The vestibular apparatus is composed of three mutually perpendicular semicircular canals and the utricle. The canals provide information on rotational acceleration, and the utricle on translational acceleration. Additionally, the utricle provides positional information of the head with respect to gravity.

IV. PRELIMINARY DYNAMICS

A. MUSCLE SPINDLE AND STRETCH REFLEX

The muscle spindle (Fig. 4) is composed of intrafusal muscle whose stretch is determined by both the state of contraction of the main muscle and the firing rate of gamma efferents innervating the intrafusal muscle. Primary and secondary afferents exit the muscle spindle and their firing rate is determined by the degree of stretch of the intrafusal muscles. The above is an oversimplification but will suffice to explain the stretch reflex. The primary afferent enters the posterior horn of the spinal column and influences the firing of the alpha motoneuron innervating the corresponding main muscle. If the main muscle is stretched for any reason the primary afferent will increase its rate of firing which increases the firing rate of the alpha motoneuron and causes the main muscle to contract till the initial firing rate of the primary afferent is reestablished. The desired effect is to oppose any stretch of main muscle beyond its present length, as is illustrated in the following paragraph.

Figure 5 represents the bicep and tricep of the arm including spinal connections at two levels. Solid circles indicate inhibitory neurons, all others are excitatory. Referring to the figure, the basic stretch reflex for the bicep is accomplished through neurons (1) and (2); for the tricep,

neurons (4) and (5). The basic stretch reflex taking place in an agonistic muscle is assisted by inhibiting the antagonistic muscle. For example, assume an external force attempts to extend the slightly flexed arm. The basic stretch reflex will contract the bicep via neurons (1) and (2), but note neuron (1) through inhibitory neuron (8) reduces the contracting ability of the tricep controlled by neuron (5). An interesting feature of the figure pertains to the gamma motoneurons (3) and (6). They were assumed to continue firing at a fixed rate; i.e., they were not involved in the stretch reflex, what their function is will now be discussed.

B. GAMMA CONTROL

The stretch reflex can be employed in a gamma motoneuron servomechanism to cause movement. Contraction of the intrafusal muscles by gamma motoneurons will cause corresponding contraction of the main muscles (via alpha motoneurons) through an increased firing of the primary afferents. The contraction will continue until the primary afferent firing rate is practically nill. The advantage of a gamma servo control is that muscles may be contracted to a predetermined length. It is conceivable any desired posture of the body could be achieved by modifying intrinsic activity of appropriate gamma motoneurons, and once established the stretch reflex would oppose any disturbing influence. It is known the cerebellum influences the gamma motoneurons and it is proposed the cerebellum genetically knows the various postures and

associated gamma activity required to achieve the related posture. If this is true a reflexive movement of posture could occur if the cerebellum were instructed to activate a different pattern of gamma activity. The resulting movement would be path independent; i.e., once the decision was made to change posture it would be up to the stretch reflexes to achieve system balance. This form of movement could explain the concept of "final position" where electrical stimulation of certain areas of the motor cortex appears to move a limb to a particular position regardless of original orientation.

Again referring to figure 5 for illustration. Assume a decision is made to increase the flex of the arm, this could be accomplished by increasing the rate of firing of motoneuron (3) and decreasing (6). Thus the bicep and tricep will achieve new steady state lengths through the action of the stretch reflexes attempting to reestablish system balance based on new conditions.

C. ALPHA CONTROL

Another means for effecting movement is for the alpha motoneurons to directly cause contraction of main muscles with an ensuing correction to the gamma motoneurons. This follow-up correction or tracking is logical for if the gamma motoneurons were not modified they would tend to oppose the movement (stretch reflex).

D. HIGHER REFLEXES

If any portion of the nervous system can be considered a basic building block it must be the muscle spindle with its associated stretch reflex. More complicated reflexes are integrated in the spinal cord. If more than one level is involved, passage of information is via propriospinal neurons which make up approximately half of the ascending and descending fibers in the spinal cord. Some of the more complicated reflexes include, but are not limited to, flexor, crossed extensor, postural, locomotive and scratch reflex. The aforementioned reflexes can be performed in the decorticate animal but lack purposefulness. The concept of purposefulness will be used to distinguish between reflexes and voluntary movement. It also appears voluntary movement must involve the cerebral cortex regardless of what area of the brain actually initiates specific commands.

E. SUMMARY

In summary; the stretch reflex can maintain a given posture and two means for effecting movement are available; the gamma servo mechanism (to be called gamma control) and alpha initiation with gamma compensation (to be called alpha control). Considerable disagreement exists among investigators as to whether movement is by alpha or gamma control. It is probably best to assume reflexes operate through a combination of the two methods; in particular higher order reflexes. Some

evidence exists [Ref. 4] that voluntary movement is primarily by alpha control. It is speculated that discrete voluntary movement (fingers, hands, toes, and feet), both fast and slow, is via alpha control since descending fibers from the cerebral cortex controlling these areas terminate on the anterior horn of the spinal cord. Any signals terminating directly on the motoneurons will be transmitted by the alpha first since they are composed of much larger fibers. All other descending fibers appear to terminate in the posterior horn, and signals introduced at this point are processed by internuncial cells and influence the alpha and gamma motoneurons in a not well understood manner. It is speculated rapid gross voluntary movement (arms, legs, and trunk) is probably effected by alpha control based solely on the fact it is a faster means than gamma control. Slower gross voluntary movement and "pre-positioning" is probably via gamma control.

V. THE RETICULAR SYSTEM

A. GENERAL

Scattered throughout the brain stem are diffuse neurons collectively referred to as the reticular system (Figs. 1 and 2). This collective name should be viewed as a coverup for yet undiscovered specific nuclei. The neurons of this system are an intermingling of excitatory and inhibitory types, but it appears two areas exist in which one or the other predominates. The bulboreticular facilitatory area includes the reticular system in the diencephalon, mesencephalon, pons, and the lateral portions of the medulla. The bulboreticular inhibitory area comprises the reticular system in the ventromedial portion of the medulla.

Located within the ill-defined reticular system are specific nuclei (Figs. 1 and 2). The reticular system exerts its influence on motor movement both indirectly through the specific nuclei and more directly through a descending reticulospinal tract. The reticular system is intrinsically active and appears to set the general muscle tone of the body. This is accomplished by equal modifications of gamma moto-neurons of both flexor and extensor muscles which increases muscular contraction but without movement. All of the statements in this section are based on various transections of animals, but appear to be equally applicable to the human being.

B. SPECIFIC NUCLEI

The identifiable nuclei in the reticular system which are required to integrate higher level reflexes and participate in voluntary movement will be discussed in this section (Figs. 1 and 2).

The red nucleus is composed of two portions; the magnocellular area receives inputs from the globus pallidus, reticular system, and subthalamus. Output is mainly via the rubrospinal tract to lower spinal areas and via collaterals to the reticular system. This area appears to be involved in forward and backward curvature of the neck and trunk. The area of small cells receives inputs primarily from the cerebellum, and output is mainly to the reticular system.

A number of nuclei cause certain movements upon electrical stimulation. The interconnections are not well established, thus reference will be made only to movements they produce upon stimulation. The interstitial nucleus controls rotational movements of the head and eyes. The prestitial nucleus controls raising movements of the head and body. The nucleus precommissuralis controls flexing movements of the head and body. Turning movements seem to involve reticular formation in the pontile area and mesencephalic regions.

The substantia nigra receives inputs from the globus pallidus, reticular system, and the cerebral cortex. The function is not definite, but there is evidence it influences the gamma system and is involved in "pre-positioning."

The pontile nucleus derives its input from various areas of the cerebral cortex. It is proposed the majority of input is via collaterals of the pyramidal tract though some of the pyramidal fibers are known to terminate in the nucleus. The output is primarily to the cerebellum via the pontocerebellar tract. The functioning is not too well understood but will be hinted at in later sections.

The inferior olive projects fibers to the pars intermedia and lateral hemispheres of the cerebellum. It is speculated the input is from pyramidal collaterals and the globus pallidus. The dorsal accessory olive projects fibers to the anterior vermis and pars intermedia. The medial accessory olive projects fibers to the posterior vermis, pars intermedia and the flocculo nodular lobe.

The tectum which includes the inferior and superior colliculi is not too well understood. Liberty is taken to postulate the colliculi provide necessary audio and visual information required for equilibrium to appropriate nuclei, and the cerebellum via the tectospinal tract or collaterals.

The vestibular nucleus is associated with equilibrium, and inputs are from the vestibular apparatus and fastigial nucleus. Output is to the flocculo nodular lobe of the cerebellum, reticular system, and to lower spinal areas via the vestibulospinal tract.

VI. CEREBELLUM

The cerebellum and in particular the cerebellar cortex (Fig. 6) is one of the best understood regions of the higher brain centers. The knowledge is by no means complete, but is extensive when compared to what is known about, say, the basal ganglia.

Impulses are transmitted into the cerebellum through climbing and mossy fibers. Climbing fibers (excitatory) appear to originate exclusively in the olivary complex. The mapping is "one for one"; i. e., each climbing fiber terminates on only one purkinje cell (inhibitory). Additionally, the climbing fibers can exercise dominant control of their respective purkinje cells since one incoming impulse is sufficient to cause firing. The mossy fibers (excitatory) unlike the climbing fibers don't terminate directly on the purkinje cells. Instead, these fibers terminate on granule cells (excitatory) which project parallel fibers to more than one purkinje cell. Two other sets of interneurons influence purkinje activity. The first set consists of basket and stellate cells (inhibitory); these cells are innervated by the parallel fibers, and their effect is to inhibit adjacent purkinje cells not serviced by the same parallel fibers (lateral inhibition). The net effect is to sharpen the zone of active purkinje cells. The second set consists of the golgi cells (inhibitory) which appear to limit the time duration of the active

purkinje cells. The golgi cells are innervated by both climbing fibers and parallel fibers, and the golgi output is directed to the granule cells which in effect were the original source of stimulation (negative feedback). The interested reader is referred to reference [12] for more detailed diagrams. The timing action of the golgi cells may be the source of damping; i. e., the excitatory action external to the cerebellum associated with movement may be inhibited by the corresponding purkinje cells. Summarizing to this point, it cannot be overemphasized that the sole output of the cerebellar cortex is inhibitory via the purkinje cells.

Phylogenetically the cerebellum may be divided into the archicerebellum, paleocerebellum, and neocerebellum. It is possible the expansion is correlated to the development of the cerebral cortex. The cerebellum can also be divided longitudinally into the vermis, pars intermedia, and the hemisphers. Unlike the cerebral cortex, the cerebellar cortex maintains the same composition and the only output is via the inhibitory purkinje cells. Though the cerebellar cortex is uniform, afferent and efferent fibers originate and terminate in different locals.

Climbing fiber input previously mentioned is repeated for convenience. Fibers originating in the inferior olive project onto the pars intermedia and hemispheres; from the dorsal accessory olive to the anterior vermis and pars intermedia; from the medial accessory olive to the posterior hemisphers, pars intermedia and flocculo nodular lobe. Mossy fibers

from the pontile nucleus terminate throughout the cerebellar cortex with the exception of the flocculo nodular lobe, which receives its fibers almost exclusively from the vestibular nucleus. Mossy fibers also transmit kinesthetic signals either directly from the receptors or through intermediate nuclei to the cerebellar cortex in a topographic manner.

Output is via the purkinje cells which terminate in various nuclei. The fibers from the vermis and flocculo nodular lobe project principally to the fastigial nucleus which influences spinal regions via descending fibers. Fibers from the hemispheres influence the cerebral cortex and striate body via the dentate nucleus and thalamus. The pars intermedia projects fibers to the interpositus nucleus which in turn influences higher brain centers via the thalamus and spinal regions via the red nucleus.

Based on the nuclei and pathways described it is tempting to speculate on the functional mapping of the cerebellar cortex. The flocculo nodular lobe is the oldest portion of the cerebellum and is concerned with balance. The righting reflex heavily dependent on vestibular input is probably integrated in this area. The vermis appears to be involved in overall equilibrium; meaning it can consolidate primitive equilibrium (balance) with visual, auditory, and possibly other sensory input to provide the individual with spatial orientation. The hemispheres more than likely influence posture and

phylogenetically expanded with increasing complexity of the skeletal system. The role of the pars intermedia could be to coordinate posture with equilibrium. This coordination is essential as posture and equilibrium are interdependent unless specifically blocked by voluntary commands. Another interesting aspect of the cerebellum is the double topographic mapping; i. e., one set in the anterior region and the other in the posterior region. It could be the anterior mapping is for gamma control of posture, and the posterior mapping for controlling the damping function.

VII. BASAL GANGLIA

Various investigators include different nuclei within the basal ganglia; for purposes of this paper it will include the caudate nucleus, putamen, globus pallidus, and thalamus. In general it appears the striate body (caudate nucleus and putamen) receive information from the cerebral cortex, thalamus and other brainstem centers, and projects efferents to the globus pallidus for further distribution to the thalamus, subthalamus, substantia nigra, red nucleus, and olivary complex. The basal ganglia is probably one of the least understood areas of the brain, but appears to be involved in slow gross movement. A possible clocking aspect will also be discussed in another section.

VIII. CEREBRAL CORTEX

The cerebral cortex contains three fourths of all the neurons in the entire nervous system, and communicates with the remainder via corticofugal (efferent) and corticopetal (afferent) fibers. The latter all originate or are relayed through the thalamus; whereas, the corticofugal fibers constitute a complicated network which terminate on other brain stem centers, not just the thalamus. The cerebral cortex appears to be essential for voluntary movement and involves the somatosensory and somatomotor areas (Fig. 7).

The somatosensory area is principally composed of granule cells. The anterior portion of this area is interesting as it also contains pyramidal cells and will be referred to as the sensorimotor area. It is postulated this region is phylogenetically one of the oldest regions of the cortex and is involved primarily in reflexes. It also appears reasonable to speculate as the cerebral cortex enlarged, the somatosensory and somatomotor areas diverged into two distinct areas.

The somatomotor area is composed of various sized pyramidal cells, and consists of two regions; the motor and premotor, the distinction is based on the fact the largest cells (betz) occur principally in the motor region. Electrical stimulation of the motor region normally elicits discrete movements. Stronger stimulation is required in the premotor region and usually results in more complicated movements.

The corticofugal fibers exiting the somatomotor area give rise to the pyramidal and extrapyramidal systems. The pyramidal system is composed of cortico fibers (30 percent from motor, 30 percent from premotor, 40% from somatosensory) which tend to project directly to the vicinity of motoneurons, and it is believed the function of this pathway is for all discrete movement and for rapid gross movement already mentioned in a preceding section. Transection of the pyramidal tract results in loss of discrete movement though slow gross movement is apparently unaffected.

The extrapyramidal system is poorly understood, but it appears the corticofugal fibers from the somatomotor cortex enter the striate body for processing by the basal ganglia and other brain stem centers with the final objective being to cause movement by alpha and gama control.

IX. VOLUNTARY MOVEMENT (THEORY)

A thorough search of the existing literature could lure an unwary reader into believing motor movement is well understood. However, two areas in particular involving voluntary movement are definitely not established. The first is what determines and controls elemental movement. The second question, which is closely related to the first, is what determines the sequencing of elemental movements into more complex patterns. An analogy may be made to fetch instructions in a computer, but the physiological mechanism, its location, or means of addressing are not known. The first question was first hinted at in the "cerebellum" section when it was stated the golgi cells appeared to cancel excitatory activity after a period of time. It doesn't appear logical all elemental movements should require the same amount of time for execution; but how the timing is accomplished is pure guesswork at present. The second question (sequencing) is specifically addressed by reference [6], and refers to the pattern of elemental movements as an engram. The term engram is taken here to mean a learned sequence of program steps for sequential motor activity. However, before the next step in the program is taken a check is made against the present state of the system as revealed by current sensory inputs. How this is accomplished is not known, but the engrams are probably located in the cerebral cortex, possibly intermingled with the basal ganglia.

It was mentioned earlier voluntary movement is learned or unlearned. The distinction between the two is based on the degree of supervision required for execution of the movement. It is postulated the area of the brain responsible for initiating voluntary movement (for purposes of this paper referred to as the motor control area) also performs the supervisory function. It is further proposed supervisory capacity is limited, therefore it would appear logical for a mechanism or procedure to exist that would reduce the supervision required for execution of voluntary movement. A means for how this could be accomplished (in the case of elemental movement only) will be discussed based on known physiology and some speculation (Fig. 8). It must be pointed out the movement referred to is elemental and more complicated patterns (engram) will be addressed later.

The overall concept is the number of cells participating in the somatosensory and somatomotor areas for elemental movements is variable, the cerebellum provides the means to accomplish the same movement with fewer cells by a process called learning. The amount of supervision required is related to the degree of learning achieved; i.e., unlearned voluntary movement requires full supervision, whereas learned voluntary movements require no supervision. A number of aspects will be discussed to explain the theory: learning, cerebellar control of sensory input to the cortex, activity in the motor cortex, and gamma tracking. The concept of learning will be explained with reference to Figure (8). The output of the purkinje cells is based

on signals arriving via the mossy and climbing fibers. Signals via the climbing fibers will always cause signals to be passed via the purkinjes, but signals transmitted by the mossy fibers alone may or may not cause signals in the purkinjes. It is postulated [Ref. 9] that if identical signals are transmitted via mossy and climbing fibers at the same time, the purkinje cells threshold level will be decreased. With repetition the threshold will be established at a level whereby the mossy fibers alone can cause the purkinje cells to transmit signals; this process is called learning.

The second aspect to be considered is how the cerebellum can control the amount of sensory information provided to the motor control area via the somatosensory cortex. It is assumed the thalamus could in some way filter the ascending passage of sensory information (between receptors and sensory cortex) based on the output of the dentate nucleus (this could also be similar for the interpositus and fastigial nuclei). Varying output of the dentate nucleus is dependent on two modes of operation. If the mossy fibers alone are effecting movement the dentate nucleus will be inhibited. If the climbing fibers are also involved, the inhibitory effect of the purkinje cells on the dentate nucleus will be cancelled to some degree by excitatory climbing fiber collaterals. Thus it is speculated the dentate nucleus through the thalamus can control the number of cells receiving information in the sensory cortex depending on the degree of learning in the cerebellum. It could further

be speculated the motor control area could decide how much supervision is required based on the number of active cells in the sensory cortex.

The third aspect is to analyze the required number of active cells in the motor cortex to effect movement. Directing attention to the left hand side of Figure (8) it is seen the large betz cell axon travels to the spinal cord but projects diverging collaterals to the pontocerebellar tract. The smaller pyramids also travel to the spinal cord but project collaterals to both the pontocerebellar and olivocerebellar tracts. It is assumed the betz cell threshold is lower than the smaller pyramids; this is not proved but hinted at by the fact that weak electrical stimulation of the motor area can cause movement, whereas stronger stimulation is required in the premotor area which lacks betz cells. It is postulated learned voluntary movement is any movement which can be effected by the betz cell and requires no supervision. Unlearned voluntary movement requires assistance from the smaller pyramids and involves supervision. It must be assumed even though the betz cell alone can initiate movement, it must have the assistance of the cerebellum to evoke the movement. It is further assumed the betz cell through the diverging collaterals transmits signals too weak to influence the purkinje cells. The process of learning explained earlier circumvents this difficulty by lowering the threshold whereby the mossy fibers alone can effect the movement. In actuality all voluntary movement is

probably effected through a combination of betz and varying numbers of smaller pyramids based on the degree of learning; which it will be recalled also modifies the sensory input.

The final aspect is that an appropriate spatial pattern of purkinje cells must be stimulated to provide proper gamma compensation which provides the damping function and possibly "pre-positioning."

Based on Figure (8) and the discussion to this point, loss of the cerebellar cortex would flood the sensory cortex with information, would require supervision for elemental movements, would disengage the gamma damping, and would disengage gamma follow-up for alpha controlled movement. A relevant medical history is presented to provide some insight. The subject was an individual [Ref. 8] who lost one side of his cerebellum. Functioning was normal on the intact side but jerky on the injured side. In the words of the patient himself, "The movements of my left hand are done subconsciously, but I have to think out each movement of my right arm. I come to a dead stop in turning and have to think before I start again." This statement substantiates the argument that supervision (conscious effort) is required if cerebellar assistance is not available.

At the beginning of this section it was stressed the voluntary movement being addressed was elemental. Naturally complex movements are sequenced patterns of elemental movements. Sequencing complicates matters in that it requires a clocking mechanism either of time (open loop) or system states (closed loop). It could be the basal ganglia is

a timing mechanism which gates the output of the cerebellum (open loop) with the output based on the state of the system (closed loop). Thus it appears two conditions must be met, one of timing and the other being proper sensory input to the cerebellum. It might be analogous to a computer in which the output of the cerebellum together with the engram provides the address of the next instruction, and the basal ganglia executes the fetch in addition to the timing.

The important consideration is that the patterns must be interrupted prior to completion if not being executed properly. This could be achieved by the system described in this section in that if the correct elemental movement was not performed within tolerance, increased sensory input to the motor control area would indicate supervision is required.

X. DISCUSSION

The central point of the preceding section was to theorize that learning motor movements involves the cerebral and cerebellar cortex, and the level of activity is related to the degree of learning. In this section liberty will be taken to expand on this concept on a purely intuitive basis. The ideas of prior sections are still valid but are renamed to be more appropriate for a philosophical discussion. Supervision will now be referred to as attention. The motor control area is a subset of a more general control area called the mind; no mysticism is implied, it is merely an aspect of the brain that is not understood at this time. Awareness is the knowing something is or is not transpiring, and is probably dependent on sensory inputs.

At this time the concepts of consciousness, subconsciousness, and unconsciousness will be introduced in a motor function context though the ideas are equally applicable to functions other than motor. Conscious movement is any movement that an individual has focused his attention on and is aware he has done so. Example, moving a finger to a designated word on this page. Subconscious movement is identical in outward appearance to conscious movement; the difference being the movement is being performed with awarness, but attention is no longer required. Example, while running to catch a football, attention is

focused on the intercept trajectory not on the mechanics of running. Unconscious movement is performed without attention or awareness. Example, tossing and turning while sleeping.

The mind can focus attention (supervision) on only one function at a time; but it is aware other functioning is occurring even though it ignores detailed knowledge (reduced sensory input). An example is daydreaming or thinking about abstract problems while driving a car; though the mind has its attention on intellectual activity it must also be aware it is controlling the car. The question is how can the individual drive the car without paying attention? Surely this cannot be accomplished by more highly integrated reflexes which is what some individuals claim constitutes learned activity. While the individual is driving, the brain is collecting and processing sensory input to effect responses in a manner similar to when first learning to drive (conscious level), but with sufficient practice can be performed without attention (subconscious level).

It is tempting to relate the organization and functioning of the brain to computers; which is acceptable provided it doesn't mislead or oversimplify a system that some claim will never be fully comprehended. The brain may be envisioned as a computer consisting of a master program (conscious mind) and many subprograms (subconscious mind). The master program can focus attention on only one subprogram at a time though it can allow subprograms to be run freely and be aware of

their execution. Thus it appears logical any function that can be performed on a subconscious level frees the conscious aspect of the brain for other tasks.

The final stage of development is to categorize cortical activity in a manner which might suggest appropriate EEG experiments. A certain amount of generalized cortical activity is always present in the living brain and can be described by four levels. The unconscious level is the minimum acceptable acitivity to exercise nerve cells. The next three levels are above the background activity. The subconscious level is the minimum activity to effect functioning of any form. The mind is <u>aware</u> of <u>any</u> area of the cortex operating at this level. The next level is the conscious level and the mind has its <u>attention</u> on that <u>particular</u> area. The extent of the involved area is probably dependent on the complexity of the function being executed. The final level is pain as the mind cannot handle excessive activity.

XI. CONCLUSIONS

Certain aspects of human physiology are well known, and were mentioned throughout this thesis; some briefly and others in more detail.

Individual neuronal functioning has been thoroughly investigated and so have numerous combinations of neurons which congregate to form pathways and nuclei.

The pathways and regions involved in spinal reflexes have been reasonably determined, including the role of the muscle spindle.

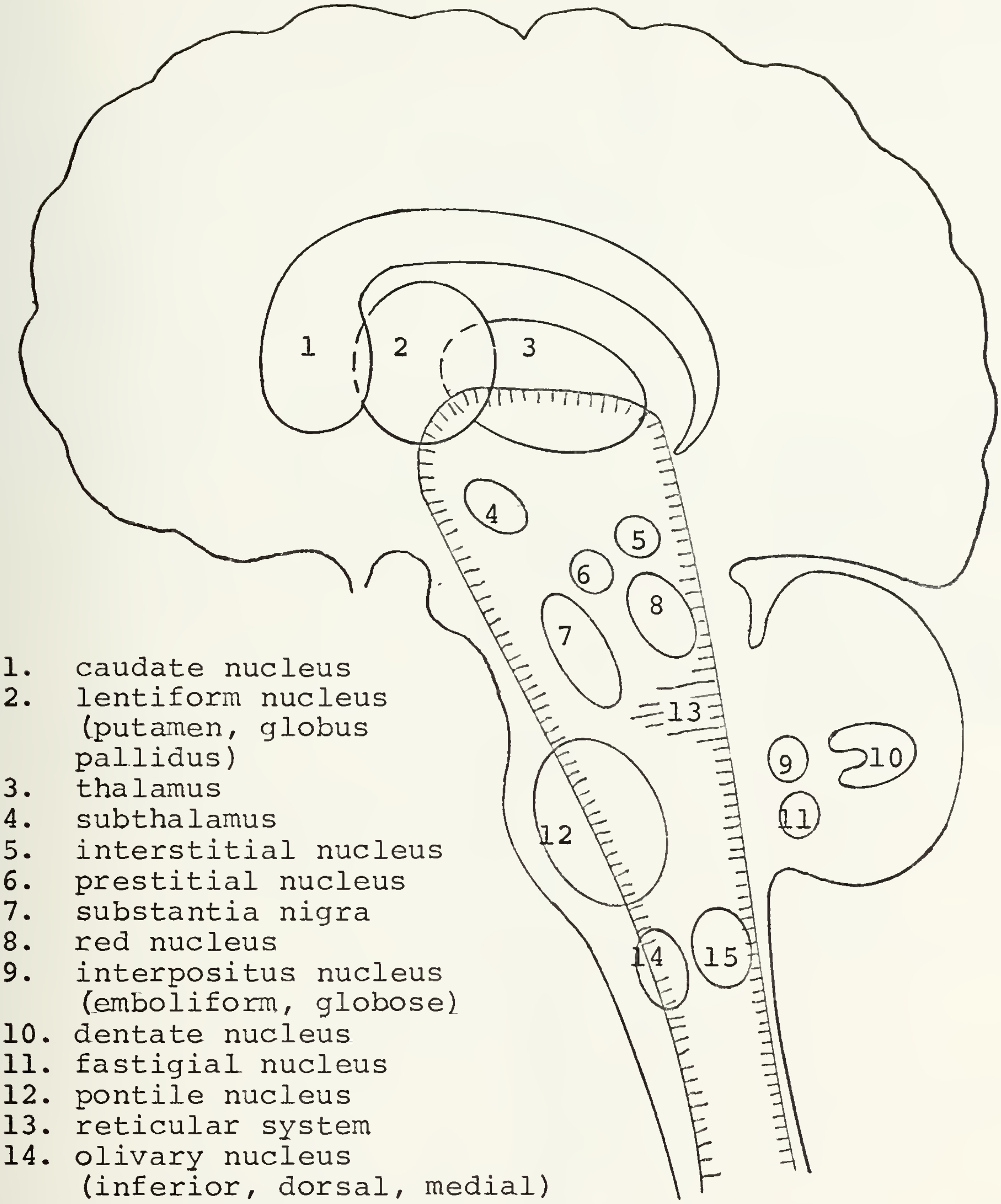
The reticular system, though not understood in its entirety, definitely establishes muscle tone and the generalized activity level in the cerebral cortex, as in wakefulness or sleep.

The cerebellum without doubt is involved in posture, balance, and the damping of movement. The cerebellar cortex is one of the first regions of the higher brain centers to be completely understood with regards to neuronal composition and interconnections.

The division of the cerebral cortex into definite regions based on function is universally accepted. The motor cortex is well mapped as to what area of the body it influences. Elemental movements can be easily evoked by electrically stimulating this region.

Though the basic building blocks of motor function are fairly well established, it is equally important to identify critically deficient areas.

The least understood portion of the brain is the basal ganglia. A more comprehensive understanding of this region will provide important insight into the programming of complicated sequential movements. Knowledge of the composition and functioning of this programming is in its infancy. Further investigation must be directed towards establishing the specific mechanisms of clocking, addressing, storing elemental movement data, and executing fetches.



1. caudate nucleus
2. lentiform nucleus (putamen, globus pallidus)
3. thalamus
4. subthalamus
5. interstitial nucleus
6. prestitial nucleus
7. substantia nigra
8. red nucleus
9. interpositus nucleus (emboliform, globose)
10. dentate nucleus
11. fastigial nucleus
12. pontile nucleus
13. reticular system
14. olivary nucleus (inferior, dorsal, medial)
15. vestibular nucleus

Figure 1. Side View Section of the Brain Showing Areas Important in Motor Control.

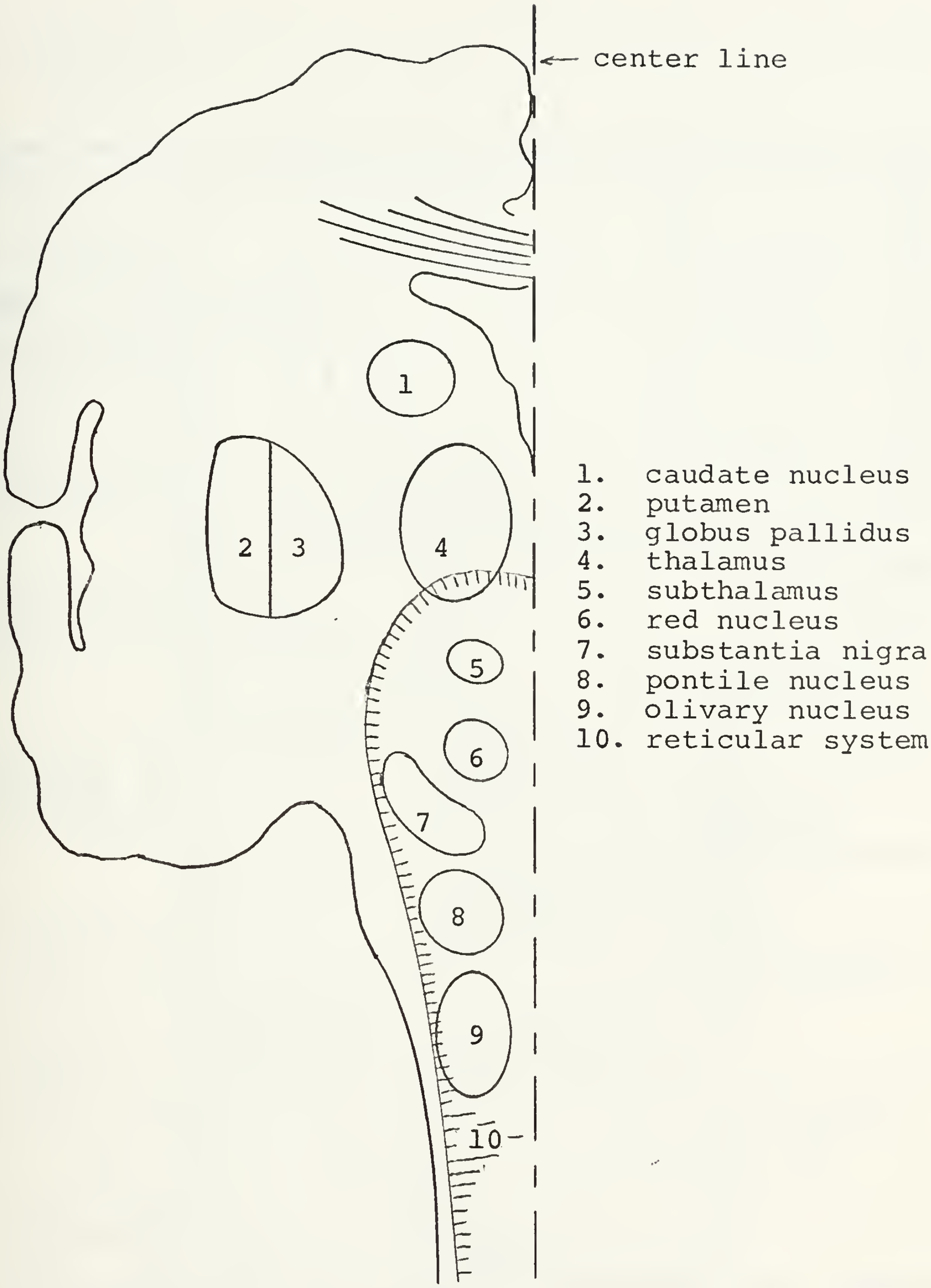


Figure 2. Section of Right Half of Brain Seen From the Front Showing Areas Important for Motor Control.

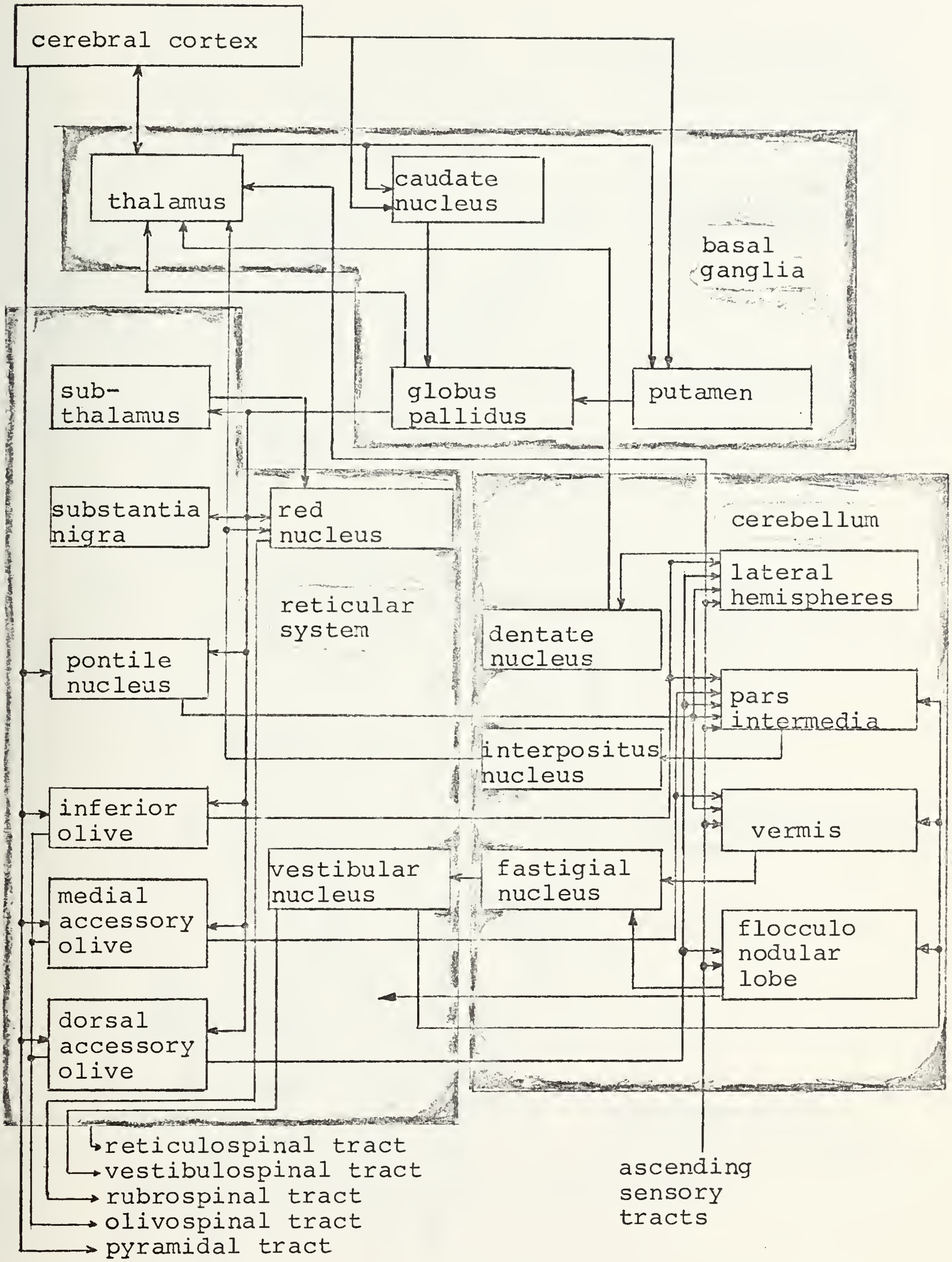


Figure 3. Signal Pathways Between Areas Designated in Figures (1 and 2), with Projections to the Spinal Cord.

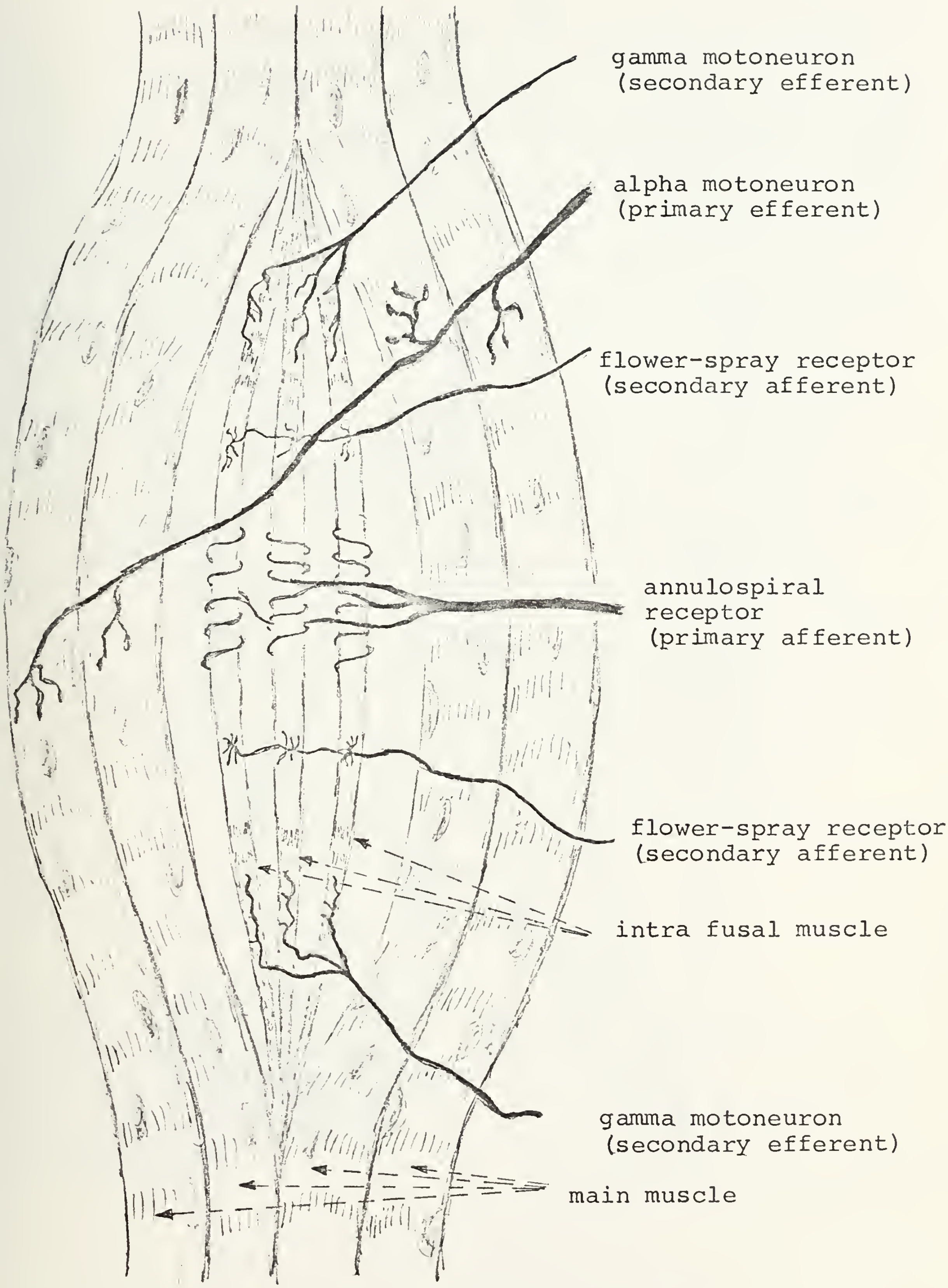
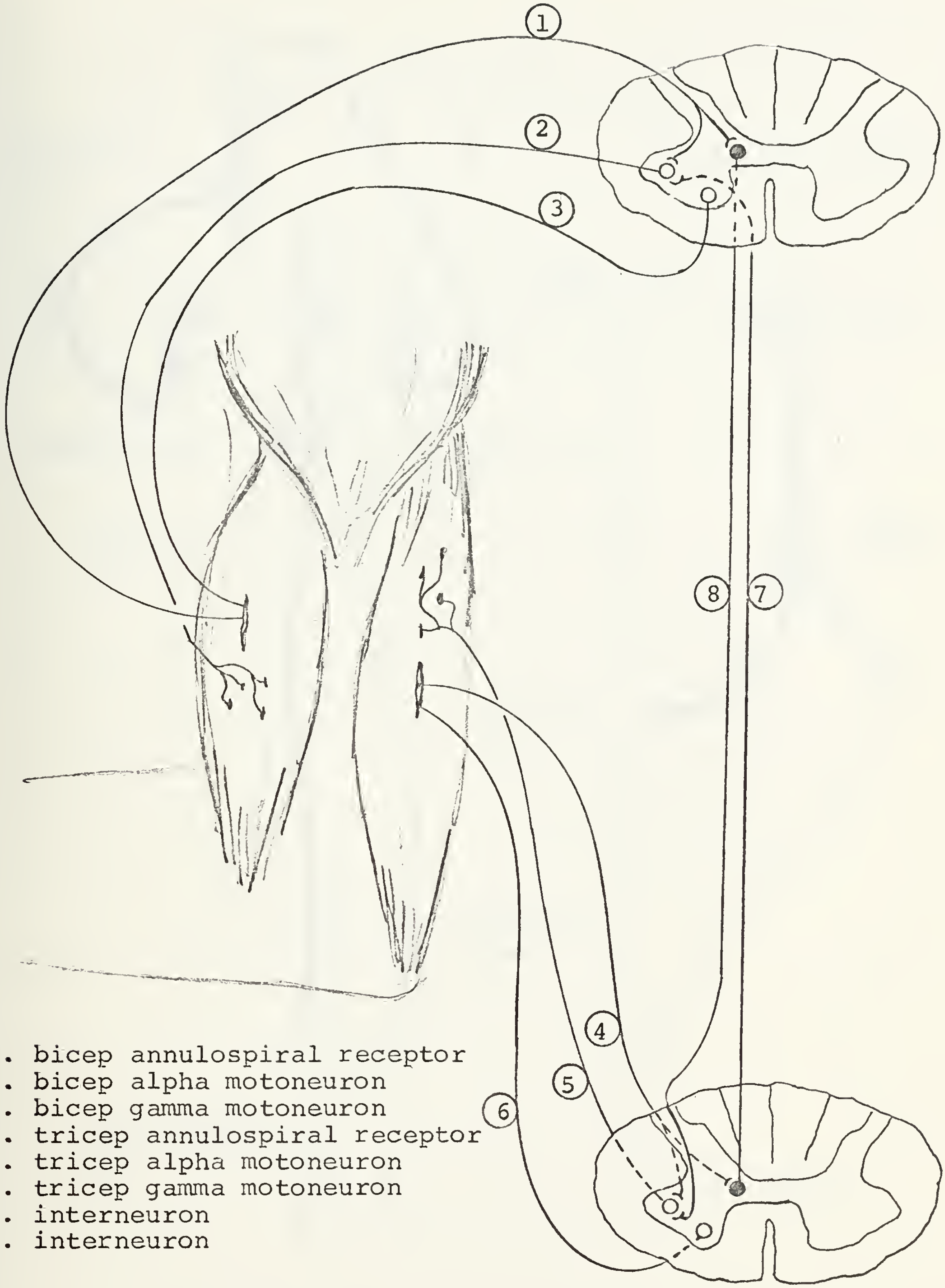


Figure 4. Muscle Spindle.



1. bicep annulospiral receptor
2. bicep alpha motoneuron
3. bicep gamma motoneuron
4. tricep annulospiral receptor
5. tricep alpha motoneuron
6. tricep gamma motoneuron
7. interneuron
8. interneuron

Figure 5. Stretch Reflex.

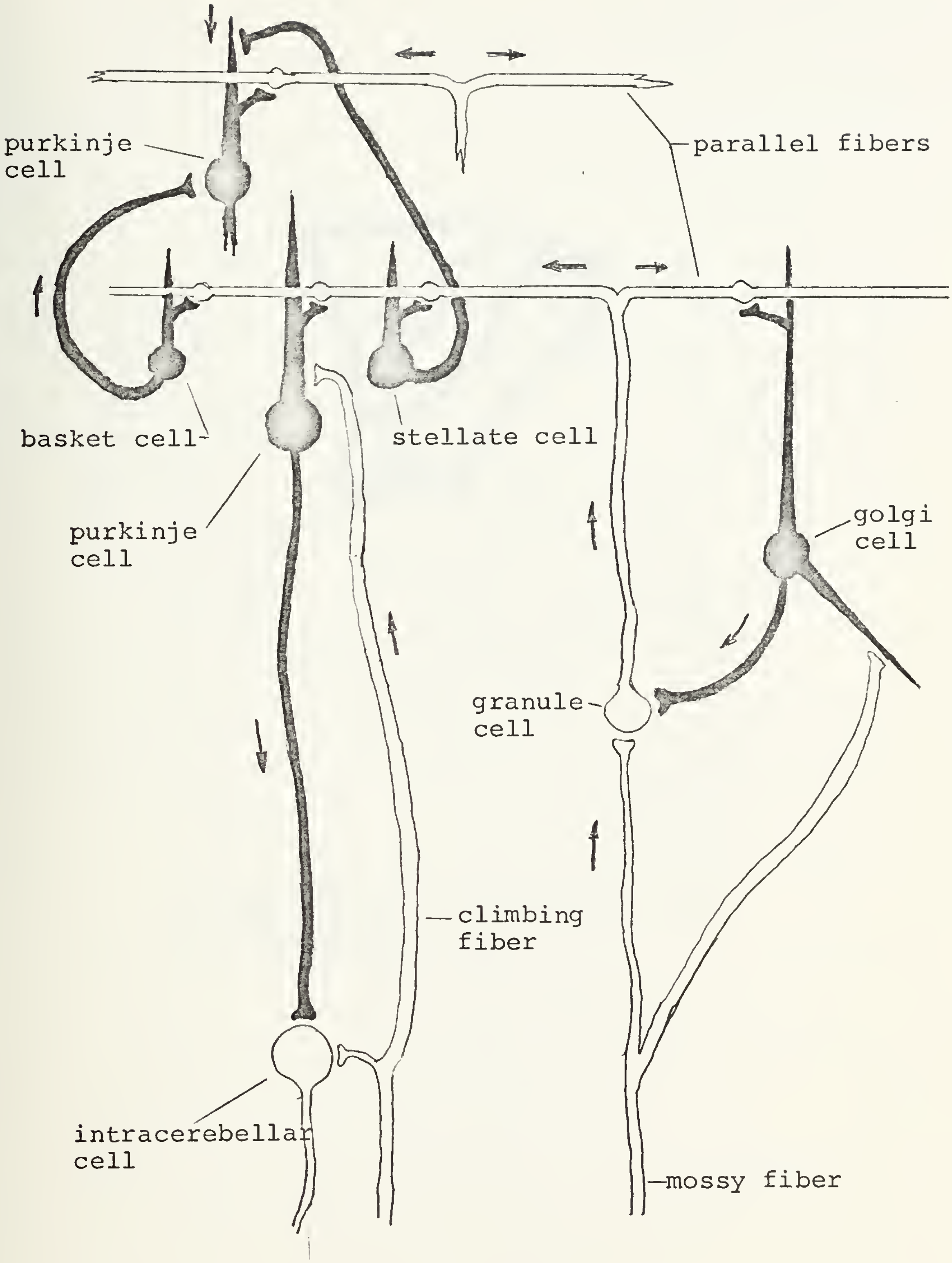
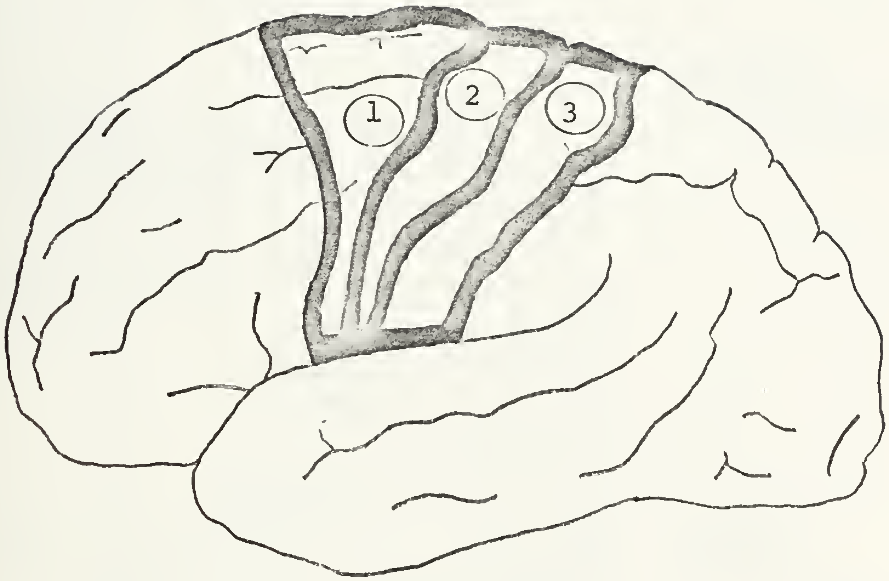


Figure 6. The Fundamental Unit Circuit of the Cerebellar Cortex.



1. premotor area ├ somatomotor area
2. motor area
3. somatosensory area

Figure 7. Left Side View of the Cerebral Cortex.

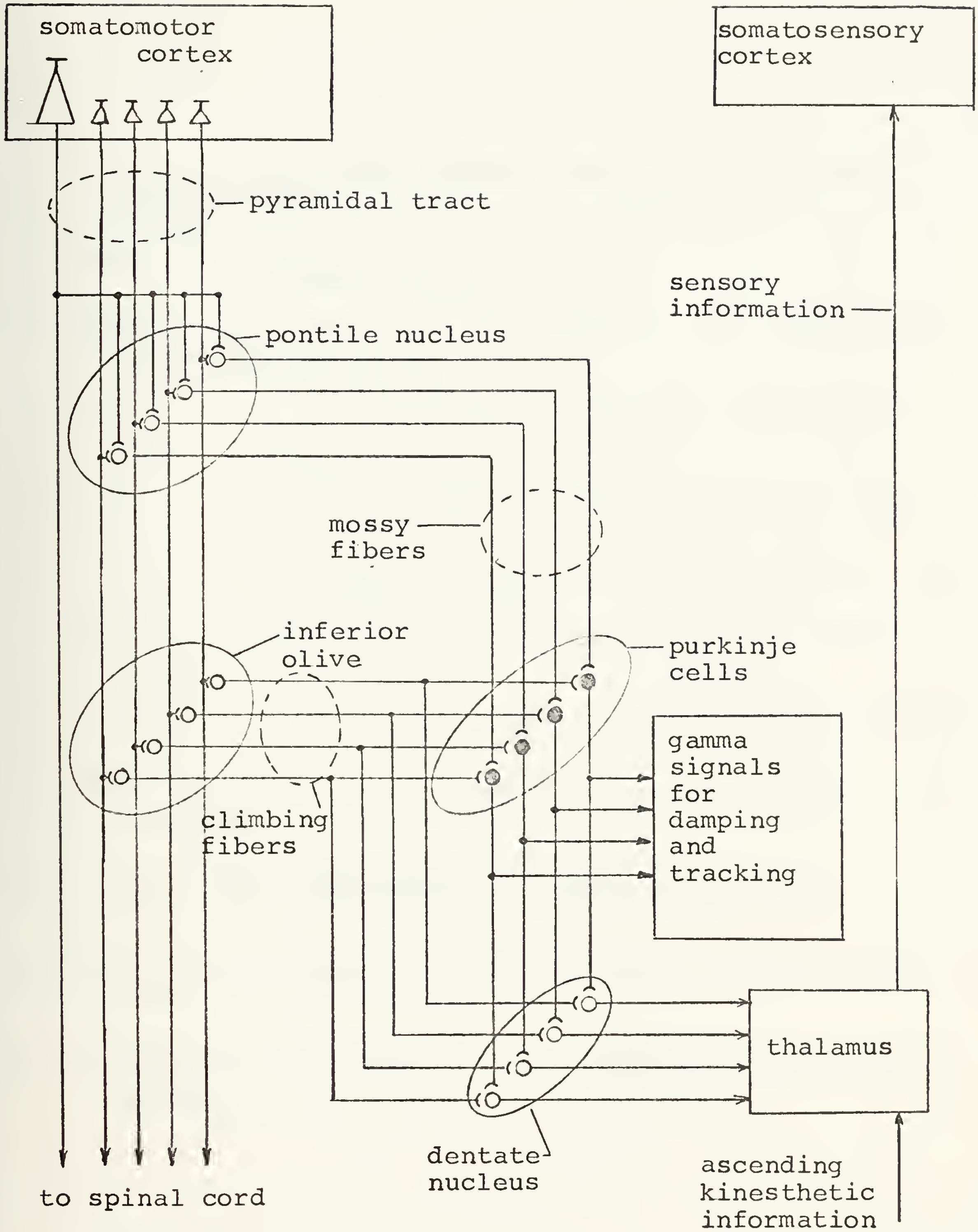


Figure 8. Diagram Indicating the Signal Pathways Involved in the Learning of Voluntary Motor Movement.

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